THE GENITALIA OF THE MALES OF CERTAIN HEMIPTERA (HETEROPTERA) AND HOMOPTERA.

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The present paper is offered as a preliminary note embodying an attempt to apply to male Hemiptera (Heteroptera) and Homoptera the terminology worked out for the genitalia of insects in general in previous papers dealing with this subject (Crampton, 1918–1920). Only a few typical forms in each group have been discussed at this time, since I am hoping to treat of these groups more extensively in a future publication. For the heteropterous material used in this investigation I am indebted to Dr. H. M. Parshley; and Professor Z. P. Metcalf and Mr. W. T. Davis have very kindly identified the Homoptera here figured. To these gentlemen I would express my very sincere appreciation of the information and assistance they have so freely given.

The following terminology of the parts of the terminal abdominal structures of male insects in general has been applied to the Hemiptera and Homoptera in the following paper. Packard, 1898, calls the abdominal segments *uromeres,* and the ninth *uromere,* which is the segment particularly associated with the genital apparatus of the male, has been termed the *gonomere* to indicate that it is the genital uromere "*par excellence*" in this sex. The terminal abdominal segments, including the segment bearing the anus, are called the *opisthomeres* by Verhoeff and other students of the Dermaptera. The ninth (or in some cases the eighth) sternite, beneath the genital apparatus of the male, is called the *hypandrium.* The cumbersome half-English, half-Latin designation "subgenital plate" or "subgenital valve" is sometimes applied to this structure in the male, but it is preferable to use a designation which would be the same in any language, as is the case with the term hypandrium. The hypandrium is occasionally produced posteriorly in two valve-like processes called the *hypovalvae.* The hypandrium also bears a pair of *styli* homologous with the exopodites of a pair of abdominal limbs whose coxae have united with the hypandrium or sternite which bore them. The styli which form the genital claspers of the male have been termed *gonostyli* (or *gonopods*) to distinguish them from the other abdominal styli (in such insects as *Lepisma Machilis,* etc.) which are not associated with the genital structures. A "connective" extends from the base of the gonopods to the base of the aedeagus in some forms. The intromittent organ of the male is called the *aedeagus.* It is usually made up of the united penis valves (penisvalvae) and may be further complicated by the outgrowth of numerous secondary structures. The aedeagus contains the *penis,* which may be membranous, or it may bear various outgrowths and formations of a chitinous nature. The homologues of these structures in the hemipteroid insects (Hemiptera and Homoptera) may be described as follows:

The GONOMERE or genital uromere of the male is formed by the homologue of the ninth uromere; but it is not always evident that the ninth uromere is the one involved, since the basal abdominal segments are sometimes atrophied, or they may unite to some extent, making it difficult to detect them in the adult stages. The gonomere bears the label "9" in the appended figures (Plate 13). It is sometimes called the "pygofers" (or "rump-bearers") by homopterists, while the dipterists call it the "hypopygium" (or "under-the-rump"), and students of other groups have applied various terms to it; but it is preferable to retain the designation gonomere, or genital segment, for the structure in question, since it is *the* genital segment of the male insect in the Hemiptera as well as in other insects.

The OPISTHOMERES bear the labels 10 and 11 in Figs. 12, 13, etc., and represent the tenth and eleventh uromeres which bear the telson—the representative of the twelfth abdominal segment. The tenth uromere (labeled *pg* in Figs. 2, 4, 5, 6, 7, 8, 10, etc.) is usually better developed than the others, which are usually telescoped within it; and since the tenth uromere is the apparent carrier of the anus, it has been termed the *proctiger.*

The PROCTIGER, or tenth uromere, within which the other terminal uromeres are telescoped, is long and slender in the insect shown in Fig. 6, *pg;* and in the insect shown in Fig. 5 it bears a shallow trench or groove *as* called the *anosulcus,* which serves to conduct off the material discharged from the anus. In the cicada shown in

Fig. 9 the tenth uromere is produced posteriorly over the intromittent organ *ae*, and its position suggests that it may correspond to the structures called the *tegumen* and *uncus* in Lepidoptera, although the tenth uromere never has the form of a tegumen and uncus in the lower insects, and is always the apparent bearer of the anal papilla. The tenth uromere of the cicada shown in Fig. 9 bears a pair of hook-like structures (one on either side of the intromittent organ *ae*) which were termed the *surgonopods, sg,* in other insects, from their position above the gonopods or clasping organs. It is possible that the structures labeled *sg* in Fig. 9 may represent the fused structures called the *scaphium* (from a fancied resemblance to a shovel or skiff) in Lepidoptera, but the surgonopods are not united in the cicadas and other related forms. I have not been able to procure the material necessary to enable me to homologize the parts of a cicada with those of the Lepidoptera, but from an examination of the material available it would appear that the structure of the terminal appendages of the male would bear out the evidence of a rather close relationship between the hemipteroids and Lepidoptera indicated by the wing venation, and a comparison of the genitalia in the two groups should be productive of interesting results. The structures labeled *sg* in Figs. 12 and 13 apparently represent the surgonopods *sg* of the cicada shown in Fig. 9, and if this be correct, it would indicate that the surgonopods arise as processes of the pleural region of the tenth uromere, possibly homodynamous (*i.e.*, serially homologous) with the pleural processes labeled *pp* borne on the ninth uromere of the insect shown in Fig. 13. It is also possible that the structures labeled *sg* in Figs. 9 and 13 may represent the cerci, but it is more probable that the interpretation indicated by the labels is the correct one. The lips of the anal opening, or *anolabii*, labeled *al* in Figs. 2, 5, 6, etc., project from the proctiger *pg*, and the telson, or the united eleventh uromere and telson, may protrude as an *anopapilla*, or anal papilla *ap*, as in the insects shown in Figs. 9 and 11.

The HYPANDRIUM or sternite beneath the genital apparatus of the male insect may occur as a distinct plate such as the one labeled *ha* in Figs. 1 and 9, or it may be indistinguishably united with the pleural region of the ninth uromere. In the insect shown in Fig. 3

a pair of posterior lobes *hv* are beginning to form in the hinder region of the hypandrium *ha,* and in the insect shown in Fig. 13 (compare also Figs. 17 and 18) these lobes have assumed the form of the hypovalvae *hv* or hypandrial valves. In the insect shown in Fig. 12 these valves become proportionately longer, and in the insect shown in Fig. 25 the hypovalvae *hv* are demarked from the remainder of the hypandrium *ha* by a faint suture. In the insects shown in Figs. 22 and 26 these valves *hv* have developed an articulation with the remainder of the hypandrium *ha,* and during copulation they fit on either side of the hypogynium or subgenital valve *hg* of the female insect as is shown in Fig. 26. The hypandrial valves *hv* of the insects shown in Figs. 22 and 26 are very similar in position, structure, and function to the valvular structures bearing the label *"s?"* in Figs. 2, 5, 6, 7, etc., but I have been unable, as yet, to obtain suitable material to enable me to determine definitely whether these two types of structures are homologous or not. The hypandrium *ha* is produced laterally to form wing-like expansions, the *parandria, pa,* one on either side of the genital apparatus of the male Hemipteron shown in Fig. 19, and the hypandrium (or rather the gonomere) forms a terminal chamber, in which the genital apparatus is borne, in the insect there figured. In the insect shown in Fig. 21 the floor of the terminal chamber bears a median ventral process *hp,* the *hypoprocessus,* which apparently serves to direct the intromittent organ in mating. In the insect shown in Fig. 16 the hypandrium is produced posteriorly to form a more or less vertical, prow-like structure *pu,* called the *puppis* in Plecoptera and other lower insects, and there are many other features of the Hemiptera which suggest that they, with the Psocida and Zoraptera, were ultimately derived from ancestors resembling the Plecoptera.

The STYLI or gonostyli *s* are borne on the posterior margin of the hypandrium *ha* of the roach shown in Fig. 20, and in the Hemipteron shown in Fig. 24, the styli or gonostyles, *s,* occupy the typical position on the posterior margin of the hypandrium *ha,* as in the roaches. The gonostyles, *s,* of the mirid shown in Fig. 24 are asymmetrically developed and bear curious outgrowths, or "prongs," suggestive of the condition occurring in certain roaches as well. In the Hemipteron shown in Fig. 23 the gonostyles, *s*, have become located further forward and more dorsally than in the insect shown in Fig. 24, while in the insect shown in Fig. 19 the gonostyles, *s*, come to lie within the so-called terminal chamber, formed by the genital segment. In the insect shown in Fig. 25 the homologues of the styli, *s*, are small and insignificant, but in the related form shown in Fig. 22 the styli, *s*, are well developed, as is true of the insects shown in Figs. 12, 13, etc. I have provisionally adopted the view that the valves labeled "*s*?" in Figs. 2, 5, 6, 7, 10, etc., represent the styli, *s*, of the insects shown in Figs. 12, 13, etc.; but it is quite possible that the structures labeled "*s*?" in Figs. 2, 5, 6, 7, 10, etc., may represent the hypandrial valves *hv* of Figs. 12, 13, 22, etc., instead, and I am inclined to accept the latter view as the more probable one. If the valve labeled "*s*?" in Fig. 7 should prove to be the representative of the hypandrial valve *hv* of Figs. 12, 22, etc., the structure labeled *bs* in Fig. 7 might be the representative of the styli, *s*, of the other forms (Figs. 12, 13, etc.), but the structure labeled *bs* in Fig. 7 would appear to be merely an outgrowth of the valve labeled "*s*?". It should be borne in mind that there can never be more than one pair of true styli borne on the sternite of a single segment, since the styli are the exopodites of a pair of limbs borne on the sternite of an abdominal segment, and there are never more than one pair of limbs borne on a single segment. The varied size and shape of the claspers "*s*?" of Figs. 2, 5, 6, etc., make them valuable structures in classification.

The GONOPLEURITES or pleural regions of the genital segment, which are labeled *gp* in Figs. 22, 25, 26, etc., are produced posteriorly to form the gonopleural lobes, or secondary clasper-like organs of the males in these insects. As is indicated in Fig. 26, these gonopleural lobes fit over the plate at the base of the ovipositor of the female, and doubtless aid in maintaining the parts in a suitable position during mating. The gonopleural lobes of the insects shown in Figs. 25, 22, etc., are apparently portions of the pleural region of the ninth uromere, but they are slightly different from the *pleuroprocessi*, *pp*, or pleural processes of the ninth uromere of the insect shown in Fig. 13. The pleural processes *pp* of the ninth uromere of the insect shown in Fig. 13 are apparently serially homologous with the pleural processes *sg* of the tenth uromere of this insect, and it is possible that the pleural processes *sg* of the tenth uromere of the insect shown in Fig. 13 may unite to form the backward-projecting portion of the tenth uromere *pg* of the insect shown in Fig. 5.

The AEDEAGUS or intromittent organ of the male is borne on the ninth uromere, and is possibly formed by the united penis valves (or by a modified penis valve) of lower insects. In a former paper (Crampton, 1920B) it was suggested that the penis valves may represent the endopodites of abdominal limbs (of the ninth uromere) whose exopodites form the genital styli. In the insect shown in Fig. 14 the aedeagus *ae* is chitinized in such a way as to give the impression that it is composed of a series of segments, and it is possible that the telescoping of these segment-like structures, one into the other, may give rise to the complicated arrangement of the aedeagus in certain insects, although the secondary formation of chitinous outgrowths, etc., have brought about this condition in other instances. In the insect shown in Fig. 4 the terminal portion of the aedeagus, called the *telaedeagus ta* in other insects, takes on the character of an articulated appendage, apparently homologous with the more ornate structure labeled *ta* in Fig. 6. The aedeagus of the insect shown in Fig. 5 bears a pair of hook-like spines, the *aedeagohami, ah,* which may be homologous with the similarly located structures labeled *ah* in Fig. 2; while the claw-like *aedeagounci, au,* of Fig. 5 may possibly be homologous with the slender structures labeled *au* in Fig. 2. It is very difficult to homologize all of the intricate, secondarily developed structures of the intromittent organ in the different types of hemipteroid insects, however, and the interpretation of these parts can be better taken up when suitable material for tracing their modifications in the various groups is available.

The PENIS is usually a retractile organ, and in most hemipteroid insects it is not protruded from the aedeagus excepting under sexual stimulus. The ejaculatory duct opens through the penis, and in such forms as the Dermaptera the terminal portion of the ejaculatory ducts may become chitinized to form the so-called virga. Various chitinizations of the integument and secondarily formed projections serve to complicate the structure of the penis; and in some instances, as in Fig. 15, it is very difficult to determine the purpose and "*modus operandi*" of certain of the curious copulatory accessories developed in this region.

It is not my purpose to discuss the relationships indicated by the terminal abdominal structures of the male insects at this time, since it is necessary to make a study of various intermediate forms not at present available before such an investigation can be satisfactorily carried out. I would call attention to certain features, however, which are readily apparent from the material at hand, and which lend additional weight to evidences of relationship drawn from other sources. The terminal structures of certain of the Hemiptera (Heteroptera) are of a very primitive type, and apparently have been retained from an ancestral condition suggestive of an origin in forms resembling the Plecoptera. This is in full accord with the evidence drawn from other sources, indicating that the Hemiptera, Psocida, and Zoraptera were eventually derived from ancestors resembling the Plecoptera in many respects—although the Plecoptera do not represent the actual ancestors of these forms. In some respects the Hemiptera (Heteroptera) have retained a more primitive condition than the Homoptera have with regard to certain of the terminal structures; but, in general, the Homoptera are more primitively organized than the Hemiptera (Heteroptera). As I am hoping to show in another paper dealing with this subject, the terminal structures of certain Hemiptera are extremely similar to those of certain Psocida, thus bearing out the conclusion drawn from the study of other structures which would indicate that the ancestors of the Hemiptera and those of the Psocida were very similar in many respects—although the Psocida can not be regarded as the actual ancestors of the Hemiptera. There are many features of the terminal structures of male Hemiptera which suggest affinities with the Blattida (*sensu lato*), and the character of certain other features, such as the wings, etc., would indicate that an investigation of this matter further may lead to interesting results in determining the nature of the forms ancestral to the Hemiptera, Psocida, Zoraptera, etc. Furthermore, a comparison of the genitalia of male hemipteroid insects with those of male Lepidoptera indicates that there is a marked similarity in these structures in both groups, so that the pronounced resemblance between the wings of certain Homoptera and the Lepidoptera may not be wholly due to convergence, and a study of Homopteron anatomy may throw considerable light upon the question of the nature of the ancestors of the Lepidoptera (which would also involve a study of the Psocida in this connection).

The genital and terminal structures of a cicada (Fig. 9) are not as primitive as one would expect from the fact that the cicadas are placed among the lowest of the Homoptera. In fact, the terminal segments of a cicadellid (jassid), such as the one shown in Fig. 13, have remained in a more primitive condition than is true of the average cicada, and the membracid shown in Fig. 1 is more primitive in this respect than the cicada shown in Fig. 9. The membracids resemble the cicadas in having a distinct hypandrium *ha* (Figs. 1 and 9), but in other features the membracids do not resemble the cicadas as much as one would expect from evidence of relationship furnished by structures other than the terminal abdominal ones. The cercopid shown in Fig. 3 has much in common with the membracids such as the one shown in Fig. 1, but the resemblance between the two groups is not very striking. The psyllids (Fig. 4) appear to be as near the fulgoroids (Fig. 6) as any other Homoptera, so far as their terminal abdominal structures are concerned; but it is necessary to take into consideration a far wider series of forms than those here figured in attempting to determine the interrelationships of the different hemipteroid groups, and this phase of the subject will therefore be left to be taken up in the more detailed discussion of the genitalia and terminal abdominal structures of male hemipteroid insects, which I am hoping to present in a subsequent paper.

Bibliography.

1899. **Bluemml.** Genitalorgane der Psylloden. Ill. Zeit. Ent., 4, p. 305.

1918A. **Crampton.** Terminal Structures of Males of Lower Insects. Bull. Brooklyn Ent. Soc., 13, p. 49.

1918B. **Crampton.** Same of Higher Insects. Psyche, 25, p. 47.

1919. **Crampton.** Same of Sawflies. Proc. Ent. Soc. Washington, 21, p. 129.

1920A. **Crampton.** Same of Hemiptera and Related Forms. Psyche, 27, p. 34.

1920B. **Crampton.** Basic Plan of Terminal Abdominal Structures of Male Insects. Can. Ent., 52, p. 178.

1917. **Funkhouser.** Membracidae of Cayuga Lake Basin. Cornell Exp. Sta. Mem. 11.

1919. **Kornhauser.** Sexual Characteristics of Membracid. Jour. Morphol., 32, p. 531.

1918. **Newell.** Genitalia of Insects. Ann. Ent. Soc. America, 9, p. 119.

1890. **Sharp.** Genitalia of Hemiptera (Heteroptera). Trans. Ent. Soc. London, 1890, p. 399.

Abbreviations.

ae..........Aedeagus, or intromittent organ.
ah..........Aedeagohami, or hami of the aedeagus.
al..........Anolabii, or lips of the anus.
ap..........Anopapilla, or anal papilla.
as..........Anosulcus, or anal groove.
au..........Aedeagounci, or unci of aedeagus.
bs..........Basal process of clasper.
gp..........Gonopleurite, or pleurite of genital segment.
ha..........Hypandrium, or sternite below genitalia of male.
hp..........Hypoprocessus, or process of sternal region.
hv..........Hypovalvae, or hypandrial valves.
pa..........Parandria, or lateral processes of hypandrium.
pg..........Proctiger, or structure bearing anal papilla.
pp..........Pleuroprocessus, or pleural process.
pu..........Puppis.
s...........Styli, or gonostyles.
s?..........Claspers homologous with styli, or hypandrial valves.
sg..........Surgonopods (cerci ?).
ta..........Telaedeagus, or terminal appendage of aedeagus.

EXPLANATION OF PLATES.

FIG. 1. Lateral view of genitalia and terminal structures of membracid Homopteron *Stictocephala lutea* Walk.
FIG. 2. Same of fulgorid Homopteron *Ricania speculum* Walk.
FIG. 3. Same of cercopid Homopteron *Clastoptera obtusa* Say.
FIG. 4. Same of psyllid Homopteron.
FIG. 5. Same of fulgorid Homopteron *Ormenis pruinosa.*
FIG. 6. Same of fulgorid Homopteron *Otiocerus degeeri* Kirby.
FIG. 7. Same of fulgorid Homopteron *Poblicia fuliginosa* Oliv.
FIG. 8. Same of cicadellid Homopteron *Jassus olitorius* Say.*
FIG. 9. Same of cicada *Melampsalta calliope* Walker.
FIG. 10. Same of the fulgorid *Cixius coleopum* Fitch.
FIG. 11. Same of Mecopteron *Panorpa nebulosa.*
FIG. 12. Same of cercopid Homopteron *Aphrophora quadrinotata* Say.
FIG. 13. Same of cercopid nymph.
FIG. 14. Same of gerrid Hemipteron *Gerris conformis* (with penis exserted).
FIG. 15. Accessory apparatus of penis of coreid Hemipteron *Chelinidea vittiger* Uhl.
FIG. 16. Lateral view of genitalia and terminal structures of reduviid Hemipteron *Zelus cervicalis* Stal.
FIG. 17. Dorsal view of terminal structures of saldid Hemipteron *Pentacora ligata* Say.
FIG. 18. Ventral view of tip of ninth abdominal sternite of same.
FIG. 19. Dorsal view of genitalia and terminal structures of pentatomid Hemipteron *Brochymena 4-pustulata* Fabr.
FIG. 20. Ventral view of ninth abdominal sternite of the roach *Ischnoptera.*
FIG. 21. Dorsal view of styli and proctiger of pentatomid Hemipteron *Tessaratoma.*
FIG. 22. Lateral view of genitalia and terminal structures of cicadellid Homopteron *Gypona octolineata* Say.
FIG. 23. Dorsal view of genitalia and terminal structures of coreid Hemipteron *Alydus pilosulus* H.-S.
FIG. 24. Ventral view of ninth abdominal sternite of mirid Hemipteron *Lopidea.*
FIG. 25. Lateral view of terminal abdominal structures of cicadellid Homopteron *Graphocephala coccinea* Foerst.
FIG. 26. Lateral view of terminal structures of male and female of the cicadellid Homopteron *Platymetopius acutus* Say.

* This specimen looks like a female, but Professor Metcalf assures me that all the Homoptera figured here are males.